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Consumption and Growth Rates of Chaetognaths and Copepods in Subtropical Oceanic Waters[1]

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ABSTRACT: The natural rates of food consumption and growth were calculated for the chaetognath *Pterosagitta draco* and the copepod *Scolecithrix danae* in the Pacific Ocean near Hawaii. The chaetognath's consumption rate was calculated using the observed frequency of food items in the stomachs of large specimens from summer samples and the digestion times from previous publications. The natural consumption rate averaged only one copepod per 24 hr, or about 2 percent of the chaetognath's nitrogen weight per 24 hr. The growth rates of both *P. draco* and *S. danae* were calculated with the temporal patterns of variations in the size compositions of the spring populations. The natural growth rates averaged only 2 and 4 percent of the body nitrogen per 24 hr for, respectively, small *P. draco* and the copepodids of *S. danae*. These natural rates were low in comparison with published laboratory measurements of radiocarbon accumulation, nitrogen excretion, and oxygen respiration of subtropical oceanic zooplankton.

THE RATES OF FOOD CONSUMPTION, metabolism, and growth have been determined for zooplankton in some regions of the oceans. Temperate and coastal rates have been described by Mullin (1969), Petipa et al. (1970), and Shushkina et al. (1974). Subtropical neritic rates have been measured by Beers (1964), Mayzaud and Dallot (1973), Newbury and Bartholomew (1976), Reeve (1970), and Reeve and Baker (1975). Less information is available on the rates of subtropical oceanic zooplankton, and this information is reviewed below in detail.

Perhaps the main reason for the lack of determinations of the functioning rates of subtropical oceanic zooplankton is that the methods of measurement are difficult and/or indirect. Laboratory culture is difficult with natural oceanic foods at low environmental concentrations; little growth and poor survival are obtained in such cultures. Experiments are usually run with no food or with abundant food, which yield basal rates and maximum rates because the rates of functioning of most zooplankton are dependent upon food concentration (Ikeda 1976, Mullin, Stewart, and Fuglister 1975, Reeve 1970). There is a need for methods of direct measurement of the natural rates of zooplankton.

Two techniques for the measurement of natural functioning rates of subtropical oceanic zooplankters were used for this study. One technique involved the calculation of the food consumption rate of a chaetognath population. The natural frequency of food items in the chaetognaths' stomachs was determined with field samples carefully collected with the quickest possible tows (30 min) throughout a whole diel period, as explained below. The diel mean consumption rate was then determined using the calculated frequency of food items in the chaetognaths' stomachs and the digestion times of prey, which have been reported previously in the literature.

The other technique involved the calculation of growth rates from the patterns of

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temporal variations in the populations' size or stage compositions. This graphical method assists in the identification of groups or cohorts of individuals in natural populations. In temperate latitudes, the graphical method has been used recently to calculate the growth rate of chaetognaths (Sameoto 1971) and tunicates (Heron 1972).

Year-round investigations of the micronekton in the subtropical Pacific near Hawaii have demonstrated spring–summer reproductive periods and the subsequent recruitment of small, but definite, cohorts of immature animals into the populations (Clarke 1973, 1974; Walters 1976). These variations in the populations' size compositions were observed regularly in the water that moves past the Hawaiian Islands. The regularity of the variations indicates synchronous patterns of reproduction and development for the populations in the Central Gyre of the North Pacific. The patterns were considered regular and distinct enough to initiate this study of the temporal variation during spring in the populations' size compositions of some smaller zooplankton species. The field sampling program was designed for the preliminary calculation of the growth rates and for development of the necessary modifications of the graphical method for subtropical, oceanic populations.

Two zooplankton species, the chaetognath *Pterosagitta draco* and the copepod *Scolecithrix danae*, were chosen for the study. The chaetognath's taxonomy, habitat, and distribution have been described by Alvariño (1965), Bieri (1959), and Sund (1959). *Pterosagitta draco* is epipelagic and relatively short (maximum body length about 8 mm); these two characteristics were generally associated with the species that had rapid consumption rates in the Black Sea (Petipa et al. 1970). *Pterosagitta draco* is cosmopolitan in subtropical, oceanic water (Alvariño 1965), and is one of the four most abundant chaetognaths around Hawaii (Bieri 1959, Hida 1957). Because of the species' abundance and possible rapid rate of consumption, *P. draco* was expected to be one of the dominant carnivores in the planktonic food web.

The copepod *Scolecithrix danae* is a calanoid with a mature body length of about 2 mm. It is omnivorous (Timonin 1971), feeding on large diatoms, blue-green algae, radiolarians, and crustaceans (Mullin 1966, Petipa et al. 1971). The species is epipelagic (Roe 1972, Vinogradov 1968) and is broadly distributed in warm oceanic waters. It is one of the ten most abundant calanoids in the Equatorial Pacific (Grice 1962) and in the southern part of the North Pacific Central Gyre waters (Park 1968) adjacent to Hawaii.

MATERIALS AND METHODS

The samples were collected at two stations near Hawaii in the southern part of the North Pacific Central Gyre. Station 1 (21° N, 158°20′ W) is about 30 km southwest of the island of Oahu; station 2 is located in the same region, about 10 km southwest of Oahu. The water depths at stations 1 and 2 were 3000 and 1000 m, respectively. The local water temperature in the upper 300 m (the habitat of the studied species) changes from 25° C at the surface to 12° C at 300 m. The local eddies circulated the surface water at the stations toward the Hawaiian Islands, according to both dynamic height calculations (Seckel 1955) and buoy observations at station 1 (R. R. Harvey, personal communication). The larval fish in the samples were typically oceanic (J. Leis, personal communication). Neritic meroplanktonic organisms were not found in the samples or in the chaetognaths' stomachs. These observations on currents and species compositions indicate that the sampled organisms probably had no interaction with the neritic community of the Hawaiian Islands.

To minimize any sampling bias on the populations' size compositions due to avoidance, all the samples were collected with 70-cm diameter Bongo nets, and settled volumes of only about 0.3 liter were filtered during each tow. The same nets, with 183- and 202-μm mesh, were always used next to each other on the Bongo frame. During each sampling period, equal numbers of samples

were collected with each mesh size, so the combined results for each time period contain no temporal bias due to mesh size.

The *Pterosagitta draco* and *Scolecithrix danae* populations were sampled by towing the nets steadily and obliquely through the whole depth range of both populations. The depth range that has been reported for *P. draco* in the study region is the upper 200 to 300 m (Alvariño 1964, Kolosova 1972), though some specimens of *P. draco* were reportedly at 600 m in the eastern tropical Pacific (Sund 1961). The *S. danae* depth range is the upper 200 m (Heinrich 1961, Hida and King 1955, Park 1968), but one report has been given of *S. danae* at 500 m in the equatorial Pacific (Grice 1962). Horizontal opening-closing tows were made at 350 m in the study area during March; the nets caught no *P. draco* or *S. danae*. For the present study, all the samples had a constant rate of descent and ascent through the upper 300 m, as measured with a depth-distance recorder (a recording depth meter and flow meter). The depth-distance records were also used to determine the exact volumes of water that were filtered (see Table 2).

Twelve samples for the determination of the frequency and type of food items in the stomachs of *Pterosagitta draco* were collected at station 2 during a 24-hr period on 23–24 August 1973. The amount of time required for rapidly sampling the upper 300 m was 30 min from start to finish, which kept the animals in the net for a 15-min mean residence time, or about 10 percent of the time it takes them to digest a food item. Consumption by *P. draco* of other animals in the net would have unnaturally increased the frequency of food items in their stomachs. Feeding in the net was probably minimal with the mesh sock that was always used on the cod end of the net. The following three observations from the present study also show that the specimens of *P. draco* probably fed little in the nets: (1) In the samples, specimens of *Scolecithrix danae* were found commonly, yet no specimens of *S. danae* were found in the stomachs of *P. draco*. (2) Calanoids, which are generally the most common oceanic copepods, were found to comprise a minor proportion of the copepods in the stomachs of *P. draco*. (3) The sizes of the copepods in the stomachs of *P. draco* were primarily smaller than the size range of copepods in the net with *P. draco*. Therefore, the frequency of food items in the stomachs of *P. draco* was probably changed little by the sampling.

The frequency of food items in 600 specimens of *Pterosagitta draco* was determined for two size ranges of the animals (5–6 and 6–7 mm), because the size and frequency of food items consumed changes during the development of *P. draco*. All the *P. draco* in each sample were examined. Food items in the mouths were not included in the data. The food items were identifiable through all stages of digestion, even when packed into pellets for defecation (see photographs of chaetognath's fecal pellets in Cosper 1973).

The pattern of temporal changes in the size compositions of the populations was analyzed with a series of 20 spring samples (see Table 2) collected at station 1 during the nights of 11 and 30 April, 21 May, and 4 June 1973. On each of the two earlier dates, two very long (12 km), oblique Bongo tows were collected; on the two latter dates, three similar Bongo tows were collected. The animals in each side of the Bongo net were treated as replicate samples because the port-starboard variation was similar to the between-tow variation; that is, the standard errors of the dates' mean abundances were similar when the samples were treated as separate replicates or combined together. Each sample was subsampled with a Folsom splitter; the mean numbers counted per sample were 91 and 97 specimens of *Pterosagitta draco* and *Scolecithrix danae*, respectively.

The technique by which the size composition of each sample was calculated will be described in detail for future reference. Total body length of *Pterosagitta draco* in each sample was measured and the data were grouped into 0.5-mm size categories. Specimens of *Scolecithrix danae* were separated into developmental stages. To distinguish the very small deviations in size compositions,

the frequencies of the animals in each size category were expressed as percentages of the total numbers, as Heron (1972) has done in a similar study. Also, the broad-scale deviations in the percent size compositions were distinguished with a running average, as Sameoto (1971) has used. The running average used with *S. danae* weighted the categories by factors of 0.25 N_{i-1}, 0.50 N_i, and 0.25 N_{i+1}, except that factors of only 0.67 and 0.33 were used with the smallest average. For *P. draco*, a running average was used that weighted the categories by factors of 0.17 $N_{i-1.5}$, 0.33 $N_{i-0.5}$, 0.33 $N_{i+0.5}$, and 0.17 $N_{i+1.5}$. Next, the averaged (or smoothed) percent size composition for each sample was combined, as explained below, with the other size compositions for the same date in order to obtain the population's mean size composition on each date.

The probable change in body length of *Pterosagitta draco* preserved in 4 percent formalin was checked carefully because of the need for accurate size measurements. Ahlstrom and Thraikill (1962) observed a large reduction at the time of preservation in the displaced volume of samples with many chaetognaths, but the same samples maintained their volume very well from 1 day to 2 years after preservation. During the present study, over 100 specimens of *P. draco* in a size group from 5.0 to 7.0 mm were measured to the nearest 0.1 mm on two dates (1 week and then 11 months) after preservation in formalin. The mean body length of this group changed less than 0.1 mm during this period. Reeve and Baker (1975) made similar observations with *Sagitta hispida*; during the week after the addition of preservative, there was a rapid reduction in body length, with a subsequent much slower rate of shrinkage. These observations suggest that *P. draco* shrank rapidly during preservation, but that there was very little change in body length of *P. draco* during the period from 1 week to 1 month after preservation, which is the time period when the present samples were measured.

The nitrogen content of both species was determined in a CHN analyzer (HP model 185). Specimens were rinsed briefly in distilled water. For *Scolecithrix danae* copepodid stages III, IV, and V from preserved spring samples, the stage: nitrogen regression was

$$\log_{10}(\text{Nitrogen, } \mu\text{g}) = 0.31(\text{Stage}) - 0.73 \quad (1)$$

where the correlation coefficient (r) equalled 0.99 for only three samples, but each sample contained 3 to 12 specimens of a single stage. The statistical significance of the slope (0.31) of the regression was determined because the exponential rate of increase of nitrogen with stage was considered the important aspect of the relationship for the growth rate calculations. A change of 1 standard deviation in the exponent resulted in only a 7 percent change in the calculated growth rate. The change due to formalin preservation was examined with *S. danae* developmental stages V, VI female, and VI male, the only stages that could be collected while alive and fresh. Though the specimens lost about 13 percent in nitrogen content with preservation, the exponent in the size:nitrogen relationship differed by only 2 percent for the fresh and preserved specimens. In other words, the change in nitrogen was about the same for each developmental stage, so relationship (1) was used without modification.

The size:nitrogen relationship for *Pterosagitta draco* was determined using fresh specimens with empty stomachs that were obtained during the summer. The mean body length per sample boat ranged from 4.5 to 7.0 mm; each sample contained five animals within a size range of less than 1.0 mm. The carbon:nitrogen ratio for all these specimens averaged 3.63. The size:nitrogen regression was

$$\log_{10}(\text{Nitrogen, } \mu\text{g}) = 4.58 \log_{10}(\text{Body length, mm}) - 2.46 \quad (2)$$

and $r = 0.99$ for four samples. The high exponent in the equation (4.58) is discussed below. A change of 1 standard deviation in the exponent resulted in a change of only 10 percent in the calculated growth rate. For calculation of the *P. draco* population biomass, 80 percent of the biomass occurred in a size range where 1 standard deviation of

TABLE 1

PERCENTAGE FREQUENCY OF COPEPOD GENERA FOUND IN THE STOMACHS OF *Pterosagitta draco*

FREQUENCY (%)	TYPES OF COPEPODS
35	*Oncaea*; copepodids of this cyclopoid
18	*Calocalanus*; copepodids and possibly a naupliar stage
18	*Microsetella*; both early and late copepodids of this harpacticoid
6	*Oithona*; copepodids of this cyclopoid
23	Partially identifiable calanoids from the families Pseudocalanidae or Paracalanidae

NOTE: The percentage frequency was determined with a collection of 17 relatively undigested copepods from over 600 *P. draco*.

the measurements was less than ± 50 percent of the mean.

RESULTS

Chaetognath Consumption

Food items were infrequently present in *Pterosagitta draco* stomachs, and only rarely was more than one item present per stomach. Copepods comprised 96 percent of the identifiable food items. The few noncopepod food items observed consisted of small chaetognaths or possible folded larvacean bodies. The types of copepods that *P. draco* consumed were determined with a collection of 17 relatively undigested and still identifiable specimens from over 600 chaetognaths (Table 1). Over one-third of the consumed copepods were members of a single genus, *Oncaea*.

The sizes of the copepods consumed were measured in order to estimate the total weight of the consumed food. Measurements were made of cephalothorax length and diameter for 37 copepods found within *Pterosagitta draco*. Linear relationships of chaetognath body length and the maximum cephalothorax length and diameter of consumed copepods had correlation coefficients (r) of 0.80 and 0.76, respectively. There was a much broader correlation ($r = 0.20$) between all the measurements of chaetognath length and copepod length. For estimation of the weight of food consumed by the different size categories of *P. draco*, the linear relationship for all the measurements was used:

$$C = 0.033(P.\ draco \text{ body length, mm}) + 0.321 \quad (3)$$

where C is the mean cephalothorax length, in millimeters, of consumed copepods. The cephalothorax lengths averaged 0.50 and 0.53 mm for copepods consumed by *P. draco* with body lengths of, respectively, 5.5 and 6.5 mm (the median lengths for the 5–6- and 6–7-mm size categories).

The frequency of food items in the stomachs of *Pterosagitta draco* was determined with 600 specimens (Figure 1). The daily time-weighted mean frequencies were 10.2 and 12.7 food items per 100 chaetognath stomachs for, respectively, the 5 to 6- and 6 to 7-mm size categories of *P. draco*. One standard deviation of the frequency measurements at several times of the day was about 31 percent of the observed frequencies.

Four hours after the time when food items were most frequent in the stomachs, tiny structureless specks of material were frequently observed in the stomachs. During the next 5 hr, there was a reduction in the concentration of the specks of material and in the frequency of stomachs containing

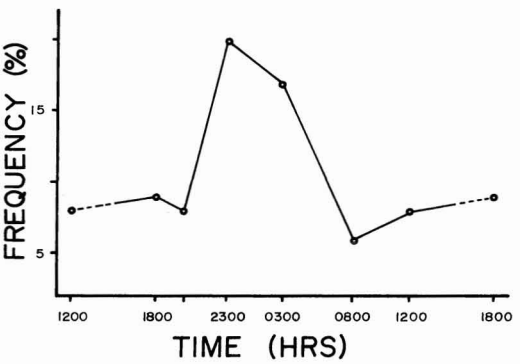

FIGURE 1. The diel variations during summer in the frequency of food items per 100 chaetognaths' stomachs for *Pterosagitta draco* 5.0 to 7.0 mm long. The diel variations were similar for the two separate size categories (5.0–6.0 and 6.0–7.0 mm), so the data have been plotted together.

TABLE 2

STAGE AND SIZE COMPOSITION OF BOTH SPECIES IN SUBSAMPLES OF THE SAMPLES TAKEN IN SPRING 1973

DATE	SAMPLE NUMBER	AMOUNT FILTERED (m^2)	*S. danae* SUBSAMPLE SIZE (1/X)	ABUNDANCE IN SUBSAMPLE OF *S. danae* COPEPODID STAGE					*P. draco* SUBSAMPLE SIZE (1/X)	ABUNDANCE IN SUBSAMPLE OF *P. draco* IN BODY LENGTH CATEGORY (mm)										
				II	III	IV	V	VI		2.5–3	3–3.5	3.5–4	4–4.5	4.5–5	5–5.5	5.5–6	6–6.5	6.5–7	7–7.5	7.5+
11 April	1	23.2	4	7	6	22	22	36	4	1	9	21	28	19	17	21	15	8	2	0
	2	23.2	8	3	1	7	9	24	2	0	2	13	17	26	22	24	17	3	0	0
	3	14.5	2	4	8	18	23	87	2	3	9	9	8	14	6	13	7	1	0	0
	4	14.5	8	4	2	6	12	44	2	0	3	9	9	11	13	17	7	1	0	0
30 April	1	28.8	8	12	18	9	8	29	4	2	8	20	19	14	13	19	18	6	3	0
	2	28.8	8	4	8	17	15	47	8	1	3	7	14	7	12	12	9	1	0	0
	3	14.7	4	3	10	21	17	68	4	0	1	9	13	16	12	8	13	1	1	1
	4	14.7	8	4	12	15	7	35	4	0	0	8	14	12	15	14	14	3	0	0
21 May	1	27.5	8	8	31	20	15	28	8	2	3	10	14	14	8	17	13	12	0	1
	2	27.5	8	3	10	13	17	20	8	0	1	5	12	12	13	10	17	9	0	0
	3	13.8	4	1	20	18	31	46	4	2	2	5	6	6	8	6	5	3	3	1
	4	13.8	8	0	2	10	22	18	4	0	2	7	10	7	9	12	17	6	6	1
	5	27.8	8	5	15	21	22	19	16	0	0	1	4	7	4	6	8	0	1	0
	6	27.8	8	0	6	26	11	8	8	0	0	5	12	15	16	15	14	7	3	0
4 June	1	34.7	8	3	15	28	18	84	8	0	3	14	15	11	9	17	18	11	1	0
	2	34.7	16	1	5	18	8	46	16	0	1	2	3	6	8	12	14	6	0	0
	3	25.8	4	1	10	22	28	92	4	0	6	8	15	12	11	36	46	6	2	0
	4	25.8	8	2	8	23	30	36	8	1	10	11	6	11	11	15	15	6	2	0
	5	32.5	4	1	17	50	71	88	4	0	5	5	17	20	20	22	46	24	12	0
	6	32.5	8	1	10	28	61	46	16	0	1	4	4	8	11	10	16	2	1	0

NOTE: Nets of 183 and 202 μm mesh were used for the odd- and even-numbered samples, respectively. The nets filtered an amount equivalent to a water column 300 m deep with the tabulated surface area, as determined with the depth-distance recorder.

them, though specks were present in some stomachs throughout the day. The specks of material have been observed in other chaetognath species in the Central Gyre (H. Lyons, personal communication). The frequency of the material was not related to *Pterosagitta draco* body size. The daily cycle suggests that the specks of material were not consumed by the large, maturing chaetognaths as food items in themselves, but were probably remains of the previously examined food items.

Biomass

The spring population biomass was calculated by combining the population size compositions in the series of spring samples (Table 2). The mean percent size composition of the total number of *Pterosagitta draco* in each of the samples (Figure 2) showed relatively low frequencies for the animals over 6.5 mm and under 3.5 mm. The rarity of the large individuals was probably accurate for the natural population, since the animals were as large (8.1 mm) as those recorded in other studies (Alvariño 1965) and there was no evidence of differential net avoidance in the frequency of large individuals from the 183- and 202-μm mesh Bongo nets. There was a difference in the mean frequency of *P. draco* in only the smallest size category (2.5–3.0 mm) from the 183- and 202-μm nets. The total biomass of the *P. draco* under 3.0 mm in size was less than 0.1 percent of the population biomass, so the observed frequencies were used without modification in the calculation of population biomass. The *P. draco* abundance during spring averaged 19 individuals per square meter of surface area for the upper 300 m of the water column. The mean abundance was multiplied by the relative frequency and nitrogen weight per animal for each size class. This yielded a mean population biomass of 135 μg nitrogen/m^2 for *P. draco*. (For estimation of the total chaetognath biomass, several measurements of dry weight of all the chaetognaths in the spring samples from the upper 300 m of the water column averaged eight times the *P. draco* dry weight.)

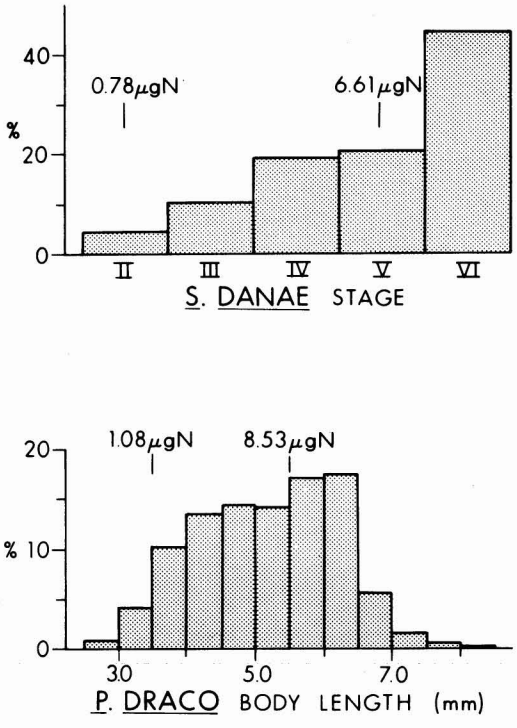

FIGURE 2. The mean size composition of *Pterosagitta draco* and *Scolecithrix danae* as percent frequency of all the animals in the spring samples. The values above the histograms indicate the ranges in nitrogen (N) weight per animals for the growth rate analyses.

The population biomass of *Scolecithrix danae* could not be calculated because the whole population was not sampled. With the stage II copepodids and younger stages, there was obvious loss through the net mesh, since fewer stage II animals were found in the samples from the 202-μm than from the 183-μm net. The frequency of the adults was high, which was probably the result of slow growth during that stage in the natural population.

Growth Rates

The temporal changes in the size compositions of *Pterosagitta draco* and *Scolecithrix danae* were examined to determine the growth rates of groups of individuals in the populations. The size range examined excluded the mature sizes when growth general-

ly slows and when the changes in the relative frequency would probably have been due to the mortality of postreproductive animals. For *P. draco*, which matures at about 6 mm, a size range from 3.5 to 5.5 mm, or from 1.08 to 8.53 μg nitrogen/animal, was examined for the growth rate determination. For *S. danae*, the size range from copepodid stages II to V, or from 0.78 to 6.61 μg nitrogen/animal, was used. The different abundance of the stage II animals in the 183- and 202-μm nets did not influence the growth rate measurements, because percent size compositions from equal numbers of 183- and 202-μm samples were combined to obtain the mean size composition for each date.

The temporal changes in the size compositions were evident when the differences were examined between the mean size compositions for the dates (DM) and the mean spring size compositions (SM). The DM was the average of the smoothed percent abundance of each weight category in the replicate samples for each date. The SM was an average of the size compositions for each date (DM), which gave the mean spring abundance for each weight category. (The means were calculated with the logarithms of the abundances, so they would be geometric and the population changes of equal magnitude would have an equal effect on the calculations.)

In a true steady-state population with constant recruitment and mortality rates, the SM should be obtained by the set of samples on each date. In the analysis, the SM were treated as zero-deviation, or reference, compositions and the patterns of deviations away from these spring means were calculated. In Figures 3 and 4, the percent deviations of the means for the dates from the mean spring size compositions [(DM − SM)/SM] are shown by the central set of points and lines. Positive or negative deviations indicate that there were more or fewer in the weight category than expected on the basis of the spring mean. The upper and lower sets of points and lines in Figures 3 and 4 indicate 1 standard error of the means for the dates that were calculated with the replicate samples for each date; that is,

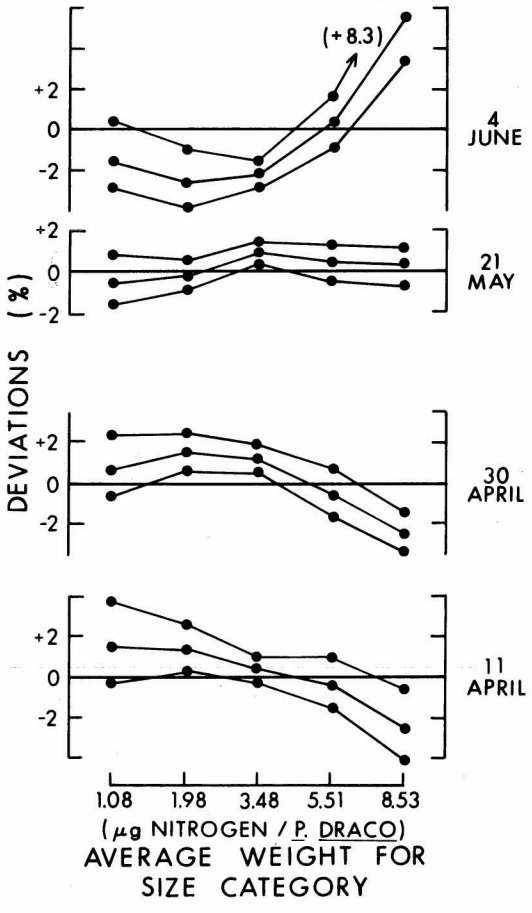

FIGURE 3. Deviations for *Pterosagitta draco* of the differences between the mean size compositions for each of the dates (DM) and the mean spring size composition (SM, represented by the horizontal, zero-deviation lines). Deviations are the percent of the mean spring number for each size category.

$$\frac{\text{DM} \pm 1 \text{ standard error} - \text{SM}}{\text{SM}}$$

where ± 1 standard error of the means equals the 68 percent confidence limit for the mean, with a normal distribution of possibilities. While the statistical significance has been calculated for each weight category on each date, the ecological significance lies in the patterns of deviations over broad size ranges for the two separate species during 2 months.

The pattern of deviations was used to measure the growth rates by identification

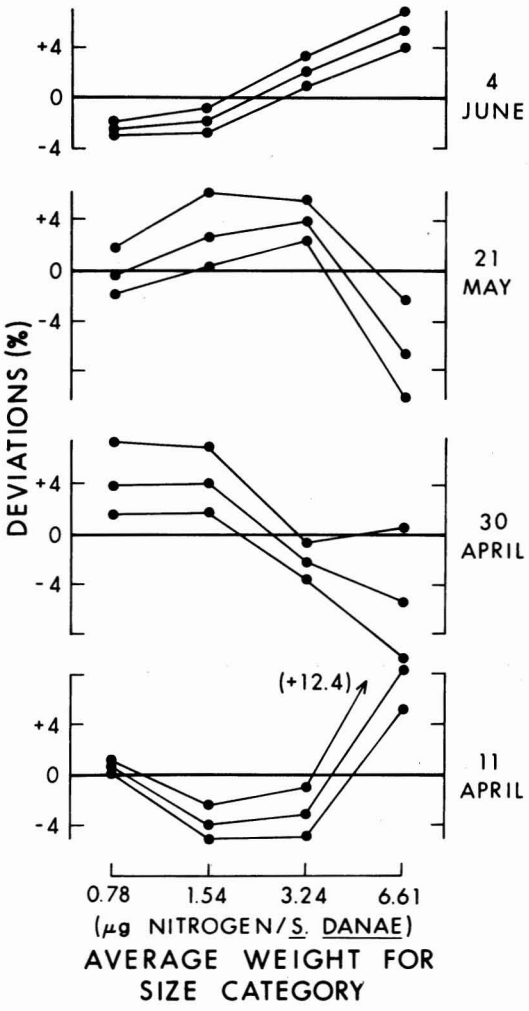

FIGURE 4. Deviations for *Scolecithrix danae* of the differences between the mean size compositions for each of the dates (DM) and the mean spring size composition (SM). The units are similar to those for Figure 3.

of similar groups of deviations or characteristics on subsequent dates. The identified characteristics were the longest, shortest, or mean size of a group, for example, with positive deviations. The growth rates were measured by the changes in size of similar characteristics on subsequent dates, as shown by the dotted lines in Figure 5. The change in size, weight increase, and geometric mean weight during each time interval are given in Table 3. The calculations of weight increase divided by the geometric mean weight and time in days were done separately for the individual characteristics to show the nature and range of variation. The calculations show that the natural growth rate:biomass ratios for *Pterosagitta draco* generally increased during the spring and that the ratios averaged only 2 percent of the body nitrogen weight per day. The calculated ratios had a standard deviation that was equal to the mean, including the statistical variation due to the species' size:weight relationship. For *Scolecithrix danae*, the variation in the growth rate:biomass ratios was inversely correlated to size and copepodid stage by the following equation:

$$\text{Daily growth rate/Biomass} = 0.08 - 0.015(\text{Stage}) \quad (4)$$

where $p << 0.01$ and df = 8. For *S. danae* copepodids, the natural spring growth rates averaged 4 percent of the body nitrogen weight per day, or two times greater than the ratio for *P. draco*. One standard deviation of the calculations for *S. danae* was 48 percent of the mean.

DISCUSSION

Estimation of the consumption rate of *Pterosagitta draco* required calculation of the chance of observing consumed food items, which is related to the portion of the day for digestion of the items. The digestion time of copepods by *P. draco* has been reported by Nagasawa and Marumo (1972) as 2.75 hr. A 2.75-hr digestion time has also been reported by Cosper (1973) for *Sagitta hispida*, a similar-sized, subtropical coastal chaetognath. The *S. hispida* observations were all made with specimens in stable laboratory cultures at environmental temperatures. Cosper observed some longer digestion times of 3 and 4 hr, perhaps because the measurements were made with chaetognaths that had consumed several copepods simultaneously. Mean digestion times of 1 and 3 hr have been measured for another subtropical chaetognath, *Sagitta enflata*, in the warm waters of Kaneohe Bay, Hawaii,

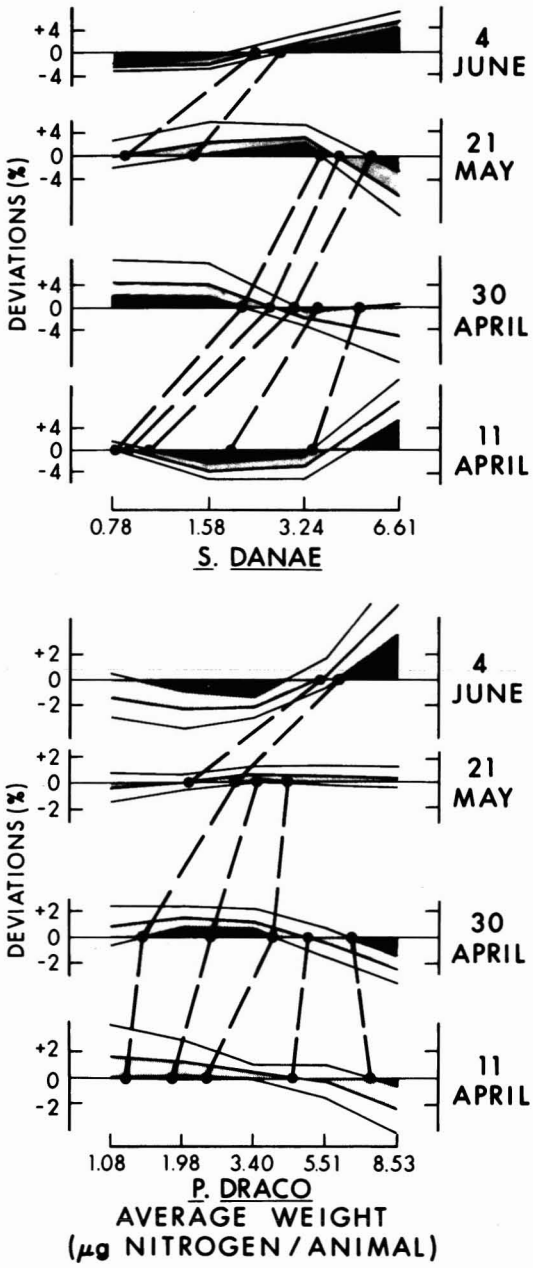

FIGURE 5. Interpretation of the temporal pattern of deviations for *Pterosagitta draco* and *Scolecithrix danae*. Light shading indicates more or fewer than expected on the basis of the mean spring size composition (SM); dark shading indicates more or fewer by a difference of 1 standard error of the means of the dates (DM). Dotted lines extend between points of similar deviations or characteristics on successive dates. The units are similar to those for Figures 3 and 4.

TABLE 3

RATIOS OF GROWTH RATE TO MEAN WEIGHT FOR *Pterosagitta draco* AND *Scolecithrix danae*

GROWTH RANGE (μg N/animal)	WEIGHT INCREASE (μg N/animal)	GEOMETRIC MEAN WEIGHT (μg N/animal)	GROWTH/ MEAN WEIGHT (day^{-1})
Pterosagitta draco			
11 April to 30 April (19 days)			
1.22–1.42	0.20	1.32	0.01
1.85–2.48	0.63	2.14	0.02
2.41–3.91	1.50	3.07	0.02
4.44–4.88	0.44	4.65	0.01
7.26–6.48	−0.78	6.85	−0.01
30 April to 21 May (21 days)			
1.42–2.99	1.57	2.06	0.04
2.48–3.47	0.99	2.93	0.02
3.91–4.19	0.28	4.05	0.01
21 May to 4 June (14 days)			
2.10–5.17	3.07	3.29	0.07
2.99–5.98	2.99	4.23	0.05
Scolecithrix danae			
11 April to 30 April (19 days)			
0.80–2.03	1.23	1.27	0.05
0.88–2.53	1.65	1.49	0.06
1.02–3.03	2.01	1.76	0.06
1.85–3.58	1.73	2.57	0.04
3.40–4.90	1.50	4.08	0.02
30 April to 21 May (21 days)			
2.03–3.70	1.67	2.74	0.03
2.53–4.21	1.68	3.26	0.02
3.03–5.37	2.34	4.03	0.03
21 May to 4 June (14 days)			
0.85–2.26	1.41	1.39	0.07
1.43–2.74	1.31	1.98	0.05

and in Florida coastal waters (Feigenbaum 1977, Szyper 1976). Longer times for digestion of copepods have been reported for a temperate chaetognath (Parry 1944) and for larger chaetognaths (Nagasawa and Marumo 1972). For *P. draco* in the subtropical Pacific, the 2.75-hr digestion time of copepods should be approximately natural. The entire 2.75-hr time period for digestion of a food item was used in the following calculations (as opposed to Nagasawa and Marumo's use of half of the digestion time) because food items of *P. draco* could be seen and counted during all stages of digestion. Multiplication of the chance of observing consumed food items (24 hr per day/2.75 hr for digestion of a food item) by the observed frequency of

food items yields a daily consumption rate of 0.89 and 1.11 items/chaetognath for *P. draco* with body lengths of 5.5 and 6.5 mm, respectively. In other words, the natural consumption rate of *P. draco* was only about one food item per day during summer in the subtropical oceanic water.

This consumption rate in terms of weight may be estimated using the nitrogen weight measurements of *Pterosagitta draco* and the collection of copepods from their stomachs. Since the consumed copepods were partially digested, their weight was estimated with the information on their size and taxonomy. The cephalothorax lengths were 0.50 and 0.53 mm for the mean sizes of copepods consumed by *P. draco* of 5.5 and 6.5 mm, respectively. Also, *Oncaea* was the main genus of copepods consumed by *P. draco*. A linear relationship was calculated between *Oncaea* cephalothorax length and wet weight using Shmeleva's (1965) data on many *Oncaea* species from another subtropical region, the Mediterranean. The wet weights averaged 15 and 18 μg/copepod for *Oncaea* with cephalothorax lengths of 0.50 and 0.53 mm, respectively. With Shmeleva's data on *Calocalanus*, another copepod consumed by *P. draco*, the calculated weights of the consumed copepods were similar (11 and 12 μg/copepod). The wet weights were converted to nitrogen weights with the dry:wet weight ratio of 0.135 for subtropical Atlantic copepods (Beers 1966) and with the nitrogen:dry weight ratios of 0.096 and 0.107 from, respectively, Beers' (1966) and Ikeda's (1974) studies of subtropical copepods from several oceans. The conversion gave mean weights of 0.21 and 0.26 μg nitrogen/animal for the copepods consumed by *P. draco* with body lengths of, respectively, 5.5 and 6.5 mm. The nitrogen weights of *P. draco* with these two body lengths are 8.53 and 18.33 μg nitrogen/animal, as calculated with equation (2). These two sets of weights indicate that both size groups of *P. draco* were naturally consuming only about 2 percent of their body weight per day during summer.

The low estimate of consumption rate is probably not due to an unreasonably low calculation of the frequency of food items in *Pterosagitta draco*. In other subtropical oceanic waters, the observed frequencies have been similar. In the Mediterranean, the most abundant species has a mean diel frequency of only 7 percent (Pearre 1974). In the Indian Ocean, only the daytime frequencies were determined (Stone 1969), but the mean daytime frequency for several species was only 3 percent, or about half the observed daytime frequencies for the present study (see Figure 1). Also, the low consumption rate was probably not due to an unreasonably high calculation of *P. draco* body weight, which was calculated using equation (2). A similar equation, with a high exponent of about 4, describes the length:weight relationship for *Sagitta hispida*, another short, subtropical chaetognath (Reeve 1966, see Figure 8). Exponents of over 3 describe the length:weight relationship for the subtropical chaetognath, *S. enflata* (Feigenbaum 1977). These studies indicate that the chaetognath's length:weight relationship and the observed frequency of food items are probably correct in the above calculation of consumption rate.

The gross growth efficiency of the chaetognath *Sagitta hispida* (Reeve 1970) is about 3:1 for the ratio of nitrogen consumed to nitrogen retained as growth. This ratio indicates that the weight-specific consumption rate should be about three times higher than the weight-specific growth rate. The actual similarity of the present rates for *Pterosagitta draco* (both 2 percent) may have been partly due to measuring of the growth rate with small, immature *P. draco* and measuring the consumption rate with large, maturing animals. The similarity may also be due to seasonal differences in the environmental food concentration and therefore in the natural consumption and growth rates of *P. draco*. The results of the consumption rate measurements, when combined with the mean population biomass of 135 μg nitrogen/m^2 for *P. draco*, indicate a consumption rate of primarily copepods of about 8 μg nitrogen/m^2/24 hr during spring.

Before the present rates are compared with the methods and results of other studies, the advantages of the present methods will be

stated briefly. Future calculations of chaetognath consumption rates obviously need better measurements of digestion times and of the weights of food items. However, the data on type and frequency of food items in chaetognaths are quite valuable because they indicate the natural feeding niches and the diel or seasonal variations in the consumption rate. This method of calculating consumption rate could also be used for other zooplankters, like heteropods, for which similar data have been collected (Hamner et al. 1975).

The primary advantage of the present technique of growth rate measurement is that the measurements were made entirely with natural populations. The importance of determinations of natural, functional rates for zooplankton was mentioned above. The field samples contained many abundant epipelagic species that may have been analyzed similarly without regard to their food requirements. For example, the growth rate (in units of only body length) was analyzed for the euphausiid *Stylocheriron carinatum* in these samples; maturing *S. carinatum* females with a body length of 3.5 mm increased their body length by an average of 1.5 percent per day. The ranges of statistical variations were not large in comparison with the ranges found in the studies reviewed below. The ranges (shown in Figures 3 and 4) indicate that samples of 5×10^4 m^3 water on each date would have allowed distinction with 95 percent confidence of the date-to-date variations in size compositions.

As stated at the beginning of this article, some laboratory measurements have been made of the functioning rates of subtropical oceanic zooplankton. These measurements are reviewed here in order to identify areas of agreements in the rates and methods.

The radiocarbon accumulation rate of subtropical oceanic zooplankton has been measured by Chmyr (1967) and Shushkina (1971). The calculated rates for both studies were based on unrealistic assumptions, as noted by Shushkina (1971) in the same paper and by Shushkina and Sorokin (1969). Another study of radiocarbon accumulation rates was performed by Petipa et al. (1971) in the southwestern equatorial Pacific during the region's summer. During one set of experiments with copepods, the herbivorous *Temora* and omnivorous *Eucalanus* were fed on radioactive, neritic plankton for 15 to 20 min and then were allowed to clear their guts of radioactive food. The maximum radiocarbon accumulation rates, or assimilation rates, for both species was equal to 11 percent of their body carbon per day. (One standard deviation of the replicate measurements for several species averaged 46 percent of the means.) During a second set of experiments, the animals' guts were not cleared, but the experiments showed that the maximum accumulation rates were similar (14 and 15 percent) for *Scolecithrix danae* and for the mean of all the individually tested copepods.

Nitrogen excretion studies of subtropical oceanic zooplankton have been completed by Eppley et al. (1973) and Ikeda (1974). The study of Eppley et al. was conducted in the fall at two locations near the present study in the North Pacific Central Gyre. The excretion rate in ng-atoms of ammonium and urea nitrogen was measured within 2 hr of capture for the unsorted surface zooplankton from a 102-μm net. The zooplankton from the 102-μm net probably consisted mainly of early copepodids (Beers and Stewart 1971). The mean excretion rate at two locations was 42 and 150 ng-atoms/mg dry weight/hr; 1 standard deviation of only the daytime measurements at each location was about 40 and 45 percent of the means. The ratio of nitrogen content to dry weight was found to average about 10 percent in subtropical zooplankton (Beers 1966, Ikeda 1974); so the weight-specific nitrogen excretion rate for the animals of Eppley et al. (1973) was probably 14 and 50 percent per day. The higher excretion rate may be due to animals that were injured in the net and were leaking nitrogen, as noted by the authors and by Mullin, Perry, Renger, and Evans (1975). The other nitrogen excretion study (Ikeda 1974) was conducted with many separate species of copepods and chaetognaths from several oceans during several months of the year. The specimens were kept in the laboratory in unfiltered seawater for 1 day before the measurements, which then

lasted for 4 to 10 hr in filtered seawater. The mean excretion rate of only ammonium nitrogen for all the copepods and chaetognaths was, respectively, 0.57 and 0.40 μg nitrogen/mg dry weight/hr. The range of 1 standard deviation in the replicate measurements was about 25 percent of the means. The rates were very size-dependent; copepod specimens with a body size similar to the large-bodied chaetognaths excreted at a slower rate than the chaetognaths. The range of excretion rates of ammonium nitrogen from Ikeda's study is similar to the range of excretion rates on only ammonium nitrogen that were measured by Eppley et al. (1973). Both studies indicate a mean excretion rate of body nitrogen of up to 50 percent per day for copepodids and small copepods, and a much slower rate for large-bodied copepods and chaetognaths.

Several studies have examined the respiration rate of subtropical oceanic zooplankton. One study (Menzel and Ryther 1961) determined the respiration rate of 366-μm net zooplankton in the Sargasso Sea. The animals' mean respiration rate was equivalent to 80 μg carbon/mg dry weight/day during the spring and summer. Since the carbon: dry weight ratio for large zooplankton in the Sargasso Sea (Beers 1966) is about 37 percent, the animals were respiring about 22 percent of their body carbon per day.

Shushkina and Vilenkin (1971) measured the respiration rates of many copepods, including *Scolecithrix danae*, a few hours after capture during summer in the southwestern equatorial Pacific. The respiration rates averaged 20 and 18 percent of the body calories per day for, respectively, *S. danae* and all the copepods. With these rates, Shushkina (1971) calculated a rate for carnivores like chaetognaths, but no direct measurements were made with them.

Another set of respiration studies (Ikeda 1970, 1974) should be compared to the previously calculated rates. The animals and laboratory techniques of Ikeda's studies have been described above. One standard deviation of the replicate respiration measurements for the following groups of species equals about 50 percent of the means. The respiration rates for chaetognaths averaged 5 μl O_2/mg dry weight/hr for the data from both of Ikeda's studies. The 1974 data gives the same mean respiration rate for the large-bodied copepods (5 μl O_2) and a slightly higher mean rate for all copepods (7 μl O_2). The 1970 data gives a much higher mean for all the copepods (29 μl O_2); even without two very high measurements, the mean rate seems unrealistically high. Excluding the 1970 data on copepods, Ikeda's respiration measurements can be compared with the other respiration studies by using the following conversion ratios for subtropical oceanic zooplankton: 4.92 cal/mg dry weight (Ostapenya and Shushkina 1971) and 4.86 cal/ml O_2 (Shushkina and Vilenkin 1971). The 1974 measurements of copepods by Ikeda indicate that the animals were respiring an average of 16 percent of their body calories per day. There is good agreement in all the mean respiration rates for copepods of 22, 18, and 16 percent from the studies of, respectively, Menzel and Ryther (1961), Shushkina and Vilenkin (1971), and Ikeda (1974).

To summarize, the weight-specific radiocarbon accumulation or assimilation rate of the copepods of Petipa et al. (1971) was equal to a maximum of 11 percent of the body carbon per day. The metabolic costs for the animals are indicated by the rates of respiration and excretion. The respiration rates averaged about 18 percent of the body calories per day; the nitrogen excretion rates (Eppley et al. 1973) were up to 50 percent of the body nitrogen per day for small copepods. These mean rates of respiration and excretion agree with the conclusion of Ikeda (1974) that subtropical oceanic zooplankton can turn over body carbon in 5 to 10 days (10–20 percent per day) and body nitrogen in 2 to 6 days (17–50 percent per day). Over these ranges, the slower weight-specific rates are characteristic of the large-bodied copepods.

The relatively high rates of respiration and excretion indicate that much of the assimilated material in subtropical oceanic zooplankton is burned for metabolic processes. The amount of material stored as growth seems relatively small according to the pre-

sent study; the weight-specific growth rate averaged only 4 percent per day for *Scolecithrix danae* copepodids in a natural population. Some of the difference is certainly due to the methods of measurement and the size of the animals, although both radiocarbon and respiration measurements (Ikeda 1976, Petipa et al. 1971, Shushkina and Vilenkin 1971) show that the *S. danae* rates are similar to the mean rates for all the copepods.

The chaetognaths' weight-specific rates are slow in comparison with the rates for copepods and zooplankton in general, as shown by the respiration and excretion measurements of Ikeda (1970, 1974) and by the natural growth and consumption rates from the present study. The mean rates for chaetognaths are similar, though, to the mean rates for large-bodied copepods. However, some large, carnivorous copepods like *Euchaeta*, *Canadacia*, and *Pleuromamma* have maximum rates of assimilation (Petipa et al. 1971) and respiration (Gaudy 1975) that are very high. The magnitude of the maximum rates suggests that these large, carnivorous copepods are more active predators than chaetognaths in subtropical oceanic waters, or that these copepods may be able to feed very rapidly (although perhaps infrequently) on patchy food sources.

Two models of subtropical, oceanic zooplanktonic food webs have been developed on the basis of the previous studies. Vinogradov et al. (1972) used a maximum consumption rate: biomass ratio of 30 percent per day for omnivorous zooplankters like *Scolecithrix danae*. Ratios of over 90 percent per day are used for microzooplankton and for carnivorous copepods and chaetognaths. The former ratio is probably correct for copepods like *S. danae*, which may use most of the consumed material for metabolic requirements, as previously mentioned. The latter ratio is perhaps correct for carnivorous copepods, but the present study indicates that chaetognaths in nature have much lower mean ratios. This difference might eliminate the need to hypothesize a high rate of cannibalism among the model's top planktonic predators (Vinogradov et al. 1974).

A model by Taniguchi (1973), based on Ikeda's (1970) study, assumes that the consumption rate: biomass ratios range from 70 to 170 percent per day for zooplankton from 333-μm nets in the subtropical oceanic water. The model has been based on unusually high rates rather than natural rates. The present study has found that the natural rates of consumption and growth for subtropical oceanic zooplankton of this size are probably quite slow.

CONCLUSIONS

1. The natural growth rate: biomass ratio averaged only 2 percent of the body nitrogen per day for small, immature *Pterosagitta draco* during the spring. The same ratio averaged 4 percent for *Scolecithrix danae* copepodids, and was inversely related to copepodid stage by the equation

$$\text{Daily growth rate/Biomass} = 0.08 - 0.015(\text{Stage})$$

2. The consumption rate of large, maturing *P. draco* averaged only 2 percent of the body nitrogen weight per day during summer. The daily consumption rate of the total *P. draco* population probably averaged 8 μg nitrogen/m^2 during spring.
3. The food items in the stomachs of *P. draco* were mainly a few genera of copepods, such as *Oncaea*. The daily mean frequency during the summer was about 11 food items per 100 chaetognaths' stomachs, which indicated a mean consumption rate of only one copepod/chaetognath/day.
4. The size composition of the natural populations varied with a consistent temporal pattern, which allowed measurement of the growth rates of groups of individuals in the populations. In order to distinguish the spring variations in these epipelagic species at a 95 percent confidence level, 5×10^4 m^3 of water needs to be filtered on each date.
5. Published laboratory rates of radiocarbon accumulation, nitrogen excretion, and oxygen respiration of subtropical oceanic

zooplankton are higher than those found in the present study. They indicate that most of the zooplankters' assimilated material is burned for metabolism rather than stored as growth. The relatively low rates for chaetognaths and high rates for carnivorous copepods suggests that the latter are the more active predators in subtropical oceanic water.

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